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Variation in sea ice cover on the east coast of Canada from 1969 to 2002: climate variability and implications for harp and hooded seals

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ABSTRACT: There is growing evidence that global change and climate variability are affecting sea ice dynamics in northern and eastern Canada. Such variability could have serious consequences for harp seals *Pagophilus groenlandicus* and hooded seals *Cystophora cristata*, which congregate to whelp on ice every February and March in the Gulf of St. Lawrence and off Newfoundland. We combined a numerical and spatial analysis of weekly averages of ice data to examine the variability of ice cover in eastern Canada during February and March, 1969 to 2002. Sea ice cover varied cyclically in eastern Canada during that time and exhibited a period of light ice years between 1996 and 2002. Spring thaw generally results in a significant reduction of sea ice cover throughout much of the study area, although some regions exhibit increases associated with oceanographic phenomena. Heavy ice years correlate with positive spring North Atlantic Oscillation (NAO) conditions and an in-depth analysis of highly anomalous (+/–) years (1970, 1972, 1981, 1993 and 2001) revealed consistent spatial and numerical patterns in ice dynamics. During light ice years, a synchronous and dramatic reduction in sea ice cover occurred in the Gulf and off eastern Newfoundland in the first and second week of March, coinciding with peak pupping periods for harp seals. Light ice years and rapid reductions in sea ice represent unquantified risks for pagophilic seals. These include increases in neonatal mortality, changes in food availability for pups and, possibly, increased risk of epizootics due to crowding on whelping patches. The magnitude of these risks may increase if observed changes in climate reduce sea ice cover in eastern Canada as they have in the Arctic. Patterns in sea ice cover and NAO conditions can be incorporated into short- and long-term management schemes aimed at ensuring the sustainability of commercially exploited pagophilic seal populations.

KEY WORDS: Harp seal · Hooded seal · North Atlantic Oscillation · Sea ice cover · Climate variability · Gulf of St. Lawrence · Newfoundland · Canada

1. INTRODUCTION

There is growing evidence that climate variability can have significant effects on various ecosystem components in the North Atlantic, from physical features like sea ice cover (Chapman & Walsh 1993), ocean currents (Taylor & Stephens 1998), and precipitation patterns (e.g. Fowler & Kilsby 2002), to biological components at various trophic levels (e.g. Post & Stenseth 1999).

Climate variability is important to the biological components of both marine and terrestrial ecosystems because many species have evolved complex life history strategies to cope with or exploit this form of environmental variability (e.g. population synchrony, see Post & Forchhammer 2002). Accordingly, the popula-

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tion dynamics of many species can be intimately tied to climate variability (Post & Forchhammer 2002), and large scale shifts in climate (e.g. ocean regime shifts or global climate change) may pose significant challenges to both individuals and their populations.

The North Atlantic Oscillation (NAO) is a large scale fluctuation in atmospheric pressure between a subtropical Azores high and a polar Icelandic low and is the dominant mode of winter climate variability in the North Atlantic region (Hurrell et al. 2003). A positive NAO phase, defined as a stronger than usual subtropical high pressure center and a deeper than normal polar low, results in more and stronger westerly winter storms crossing the Atlantic Ocean on a more northerly track. This phase produces warmer and wetter winters in the eastern USA and Europe, and colder and dryer winters in northern Canada and Greenland (Hurrell et al. 2003), representing a local (North American) North-South dipole in climatic response to NAO forcing. During negative NAO phases the opposite generally occurs, with colder winters in the eastern USA and Europe, and warmer winters in northern Canada and Greenland (Hurrell et al. 2003). The NAO has exhibited an extended period of positive phases over the past 30 yr (Gillett et al. 2003). This may stem from greenhouse-gas-related climate change (e.g. Hurrell 1995, Gillett et al. 2003), the mechanism of which is still open to debate (Gillett et al. 2003).

There is growing evidence that the NAO affects a variety of terrestrial systems in the North Atlantic region, from vegetation to carnivorous mammals (Ottersen et al. 2001, Mysterud et al. 2003). Marine systems are generally less studied, but it appears that the NAO has significant effects on a variety of trophic levels, ranging from sessile benthic organisms to migratory whales (Drinkwater et al. 2003). Rapid or extended unidirectional changes in climate may pose significant threats to many species of marine mammals, particularly those inhabiting temperate and polar regions (Lavigne & Schmitz 1990, Tynan & Demaster 1997).

One such example may be the pagophilic or ice-loving seals, such as harp seals *Pagophilus groenlandicus* and hooded seals *Cystophora cristata*, which have evolved to use seasonal sea ice in the subarctic waters of eastern Canada (Dunbar 1968)—in the Gulf of St. Lawrence and on the 'Front', off NE Newfoundland—as pupping and nursing substrate (Lavigne & Kovacs 1988). Accordingly, these animals exhibit synchronous birthing and short lactation periods (ca. 12 d for harp seals and 4 d for hooded seals) that coincide with seasonal sea ice cover (Bowen et al. 1985, Lavigne & Kovacs 1988). Changes in climate may be particularly dangerous for pagophilic seals, as variation in the quality and quantity of seasonal sea ice cover may dictate the amount of appropriate breeding habitat (Harwood 2001). Habitat availability could have significant effects on reproductive success, neonatal survivorship and possibly adult survivorship in these species (Tynan & Demaster 1997). Such cohort effects (Forchhammer et al. 2001) may be especially important for harp seals, that are currently subject to unsustainable levels of anthropogenic mortality (Lavigne 1999, Johnston et al. 2000).

While previous studies of the effects of NAO-induced climate variability on sea ice dynamics in the northwest Atlantic have focused on high-latitude regions (see Deser et al. 2002, Hurrell et al. 2003, Visbeck et al. 2003) they have not addressed rigorously the specifics of the breeding season of pagophilic seals in eastern Canada (although some information on ice conditions and seal whelping patches in certain years is available; see Sergeant 1991). Of particular interest is the spatial relationship between NAO effects and the breeding regions of harp and hooded seals in eastern Canada. The Gulf of St. Lawrence and the Front regions occupy a central position between northern Canada and the eastern coast of the USA, i.e. a position between opposite ends of the North-South dipole in climatic responses to NAO forcing in eastern North America (Drinkwater et al. 2003, Hurrell et al. 2003).

The purpose of the present study was to assess the variability in sea ice cover on the east coast of Canada during the breeding seasons of harp and hooded seals between 1969 and 2002 and to determine the extent to which this variability might correlate with NAO conditions and global climate change. Such information can be used to better understand processes governing the variation in reproductive success in pagophilic seals, and to inform management processes aimed at ensuring the long-term sustainability of their populations.

2. METHODS

2.1. Data details

Ice coverage data for the eastern coast of Canada were downloaded from the Environment Canada Ice Services website (http://ice-glaces.ec.gc.ca/) for the years 1969 to 2002. Each coverage represents the mean weekly ice-cover data during February and March for the east coast of Canada and NE USA, within the bounding coordinates of 80.34° to 36.41° W and 64.79° to 35.81° N. This area covers the 2 breeding regions for harp and hooded seals in the NW Atlantic, one located in the Gulf of St. Lawrence and the other off the NE coast of Newfoundland, commonly referred to as 'the Front.' The sea ice data are derived from a combination of remote sensing and direct sampling of the area for ice cover. For the purposes of this paper, we define sea ice cover as the total numerical concentration of ice recorded for polygon areas in each given coverage, following standard World Meteorological Organization (WMO) 'egg' codes. All ice coverages were downloaded as Arc Interchange files and imported into ArcInfo 8.1. An automated script exported the ice concentration tables into an Access database where they were summarized and read into SPSS for Windows 11.5 for statistical treatment in the numerical analysis.

2.2. Numerical analysis

To conduct the numerical analysis, we exported each weekly mean ice coverage (excluding icebergs and fast-ice) and multiplied the total area by its corresponding numerical concentration value (n_ct). The n_ct value represents the percentage (in tenths) of each ice polygon that was covered with ice. These areas were then summed for each weekly coverage to produce a mean weekly total area of ice coverage in the study area. Appropriate weeks were combined and averaged where needed to calculate the total and mean area of ice cover for the months of February and March over all years and means for each year. These data were compared statistically by year and month with a univariate General Linear Model (GLM) procedure. The total ice coverage for each year was compared against the overall mean amount of ice cover for the entire study to determine the timing and magnitude of anomalous years. From this analysis we chose 6 extreme anomalies (3 positive: 1972, 1985, and 1993; and 3 negative: 1970, 1981 and 2001) for subsequent in-depth numerical and spatial analyses. We avoided using 1969, the lowest ice year on record and focused on comparative positive and negative anomalies from the entire study period. We conducted an autocorrelation time series analysis to determine the periodicity of yearly variation in ice cover relative to the mean. To assess the rate of change in ice cover from February to March for each anomalous year, plots were generated showing the total ice cover in each of the 8 wk of the study period.

2.3. Spatial analysis

We used the n_ct of ice cover, to determine the spatial distribution of variability in sea ice coverage throughout the study area from 1969 to 2002. Each weekly ice coverage was imported into the GIS and converted into a grid with a cell size of 500 m based on the n_ct value. Thus, each 500 m cell has a value reflecting the total percentage of ice concentration within it. Weekly grids were then averaged into monthly grids for each year and a mean ice cover grid for the east coast of Canada from 1969 to 2002 was also generated. Subsequently, we generated mean ice cover grids for anomalous years and compared them to the overall mean sea ice cover. We calculated an average for all February and March measurements to assess the average spatial distribution and magnitude of ice-cover change in the study area during the spring thaw. We calculated the change in sea ice cover from February to March for each extreme anomaly year and compared these to the overall mean extent and magnitude of the spring thaw.

The Raster Calculator and Cell Statistics functions of the Spatial Analyst Toolbox were used for all calculations and comparisons between months and years. All data were projected for analysis using the Clarke 1866 Lambert Conformal Conic projection.

2.4. North Atlantic Oscillation

NAO index data were obtained from the National Weather Service's Climate Prediction Center (www.cpc.ncep.noaa.gov/). NAO values are calculated using a rotated principal component analysis (RPCA) to create a teleconnection pattern for all months (Barnston & Livezey 1987). These NAO indices (+/–) are relative to monthly mean 700 mb pressure anomalies for a 3 mo period. Treating monthly values as dependent on measurements both before and after, combined with the RPCA being based on large areas (rather than from pressure anomalies measured at a few selected locations), accounts for variability in the structure and amplitude of the NAO teleconnection pattern and allows for better continuity from month to month over longer time series (National Weather Service, Climate Prediction Center). We extracted the February–March signature from the overall data set for comparison with synoptic spring sea ice cover data, hereafter referred to as the FM NAO.

To test for correlation between mean yearly sea ice cover variability and the FM NAO index, we conducted a cross-correlation time series analysis. This method allows one to visualize the placement, or displacement, of one time-series pattern relative to another. In this case, we used a differencing of 1, where the previous value is subtracted from the current value to calculate the difference between successive values of each variable. This transformation is useful for assessing autocorrelated ecological data sets trending in similar ways (Friedland et al. 2003).

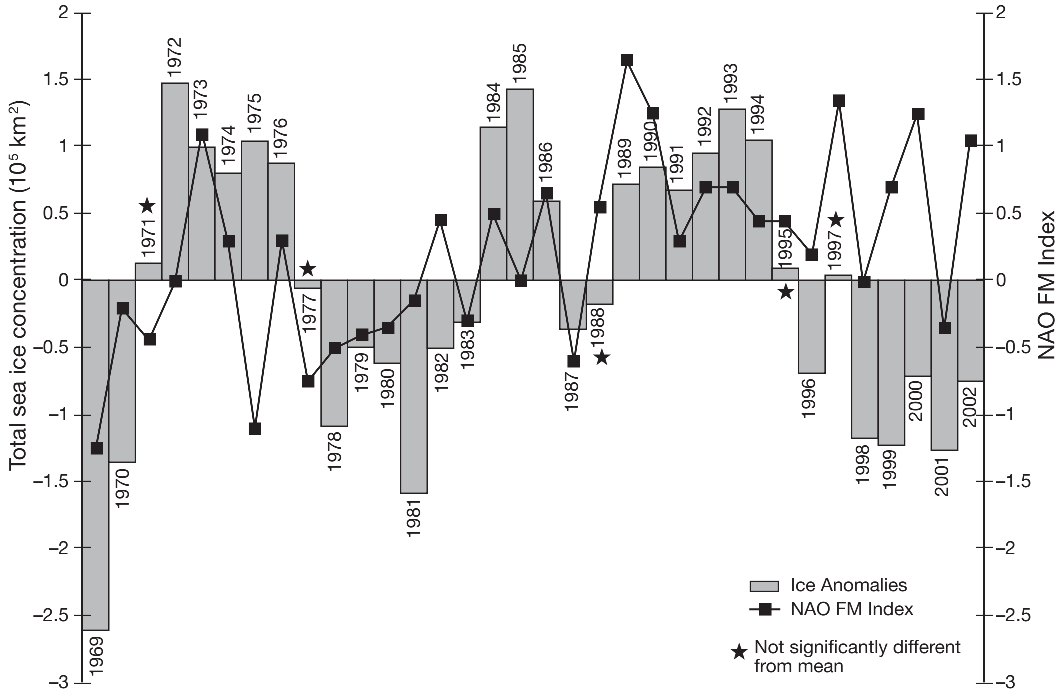

Fig. 1. Mean yearly anomalies in numerical sea ice cover for eastern Canada during 1969 to 2001, derived from weekly mean sea ice coverages with yearly FM NAO index values superimposed. Asterisks indicate yearly anomalies that are not significantly different from mean sea ice cover in the study area

3. RESULTS

3.1. Numerical analysis

The overall GLM was significant ($p < 0.01$) with both Month and Year factors identified as significant effects ($p = 0.017$ and $p < 0.01$, respectively). As well, there was a Year × Month interaction which approached statistical significance ($p = 0.068$). The total amount of sea ice annually present in the study area was variable (Fig. 1). Yearly contrasts in the GLM revealed 14 yr with significantly more sea ice than average, and 14 yr with significantly less sea ice than average ($p < 0.05$; 2002 was excluded from the statistical test as required by the yearly contrast procedure in the GLM). There appeared to be some periodicity to the amount of sea ice present: mean ice cover was significantly lower over the last 4 yr (and 5 of the last 6), preceded by 6 yr with significantly greater than average ice cover (Fig. 1). The autocorrelation plot (Fig. 2A) revealed that yearly mean ice cover data were autoregressive, and that the most significant difference in sea ice cover occurred at 6 lags. Thus, the greatest difference between high and low ice years occurred at 6 yr intervals.

The results of the GLM indicated a significant difference in sea ice cover between February and March. Between 1969 and 2002, mean ice cover across the entire study area was significantly higher

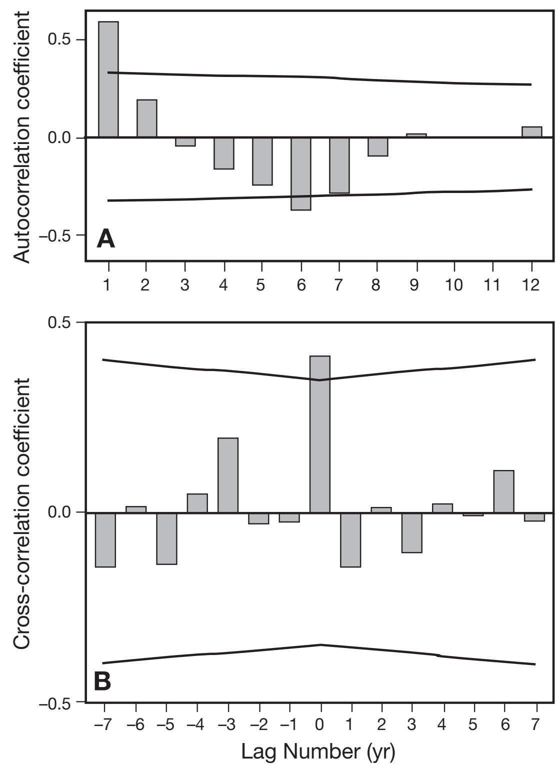

Fig. 2. (A) Autocorrelation and (B) cross-correlation time series plots for numerical sea ice cover and FM NAO anomalies during 1969 to 2002. Lines represent 95% confidence limits for coefficients

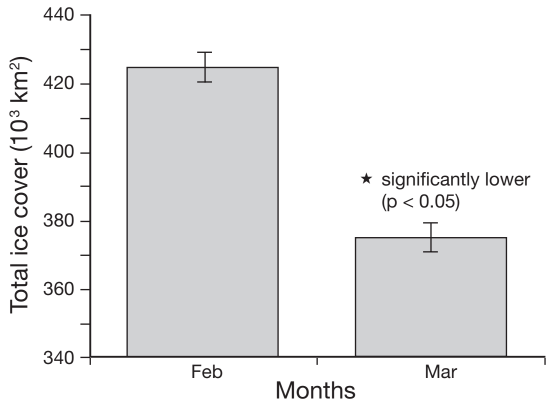

Fig. 3. Mean numerical sea ice cover in eastern Canada during February and March, 1969 through 2002. Asterisk indicates a significant reduction in sea ice cover from February to March over the entire study period. Error bars are SE

in February than in March ($p < 0.05$) (Fig. 3). This reflects the spring thaw, details of which were revealed in the weekly ice cover totals within a given extreme anomaly year (Fig. 4). In light ice years, a rapid decrease in ice cover occurred from Weeks 5 to 6 (Fig. 4A,C,F). There was less change in total ice cover from February to March in heavy ice years (Fig. 4B,D,E).

While there was substantial variability in sea ice cover over the course of the study period, there was a correlation when the FM NAO index was superimposed (Fig. 1). In general, higher (or positive) FM NAO indices occurred in heavy ice years while lower (or negative) indices occurred in lighter ice years relative to the mean. The most apparent deviation in this pattern occurred during the string of negative sea ice cover anomalies between 1995 and 2002. The cross-correlation analysis (Fig. 2B) validated this qualitative assessment, revealing a synoptic significant positive correlation (cross correlation function [CCF] = 0.42, $p < 0.05$) between sea ice cover and the FM NAO index.

3.2. Spatial analysis

The results of the spatial analysis are presented in Figs. 5 & 6. General spatial patterns in yearly sea ice cover anomalies and reductions in sea ice cover during the spring thaw are summarized in Table 1.

The spatial distribution of mean sea ice cover from 1969 to 2002 is presented in Fig. 5A. The area adjacent to the coast of Labrador was completely (90 to 100%) covered with sea ice, with concentrations

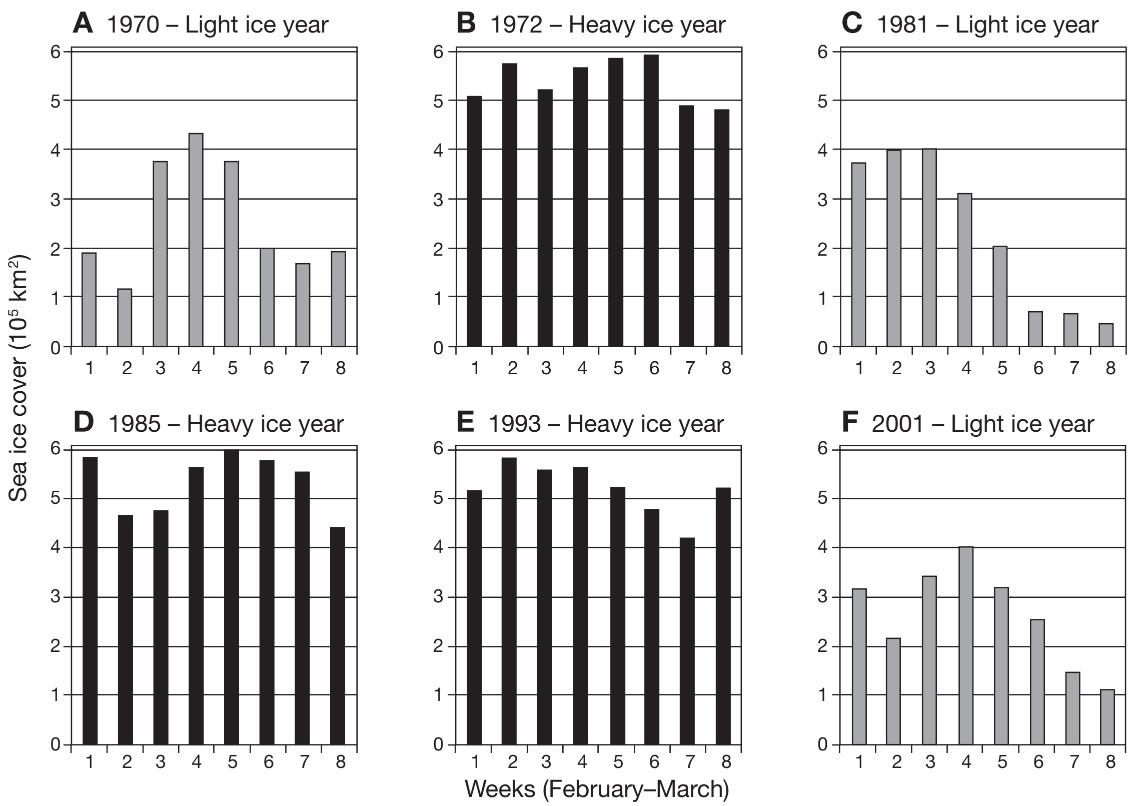

Fig. 4. Weekly numerical means in sea ice cover in eastern Canada during February and March. Light ice years (A, C and F) are indicated by grey bars, heavy ice years (B, D and E) are indicated by black bars

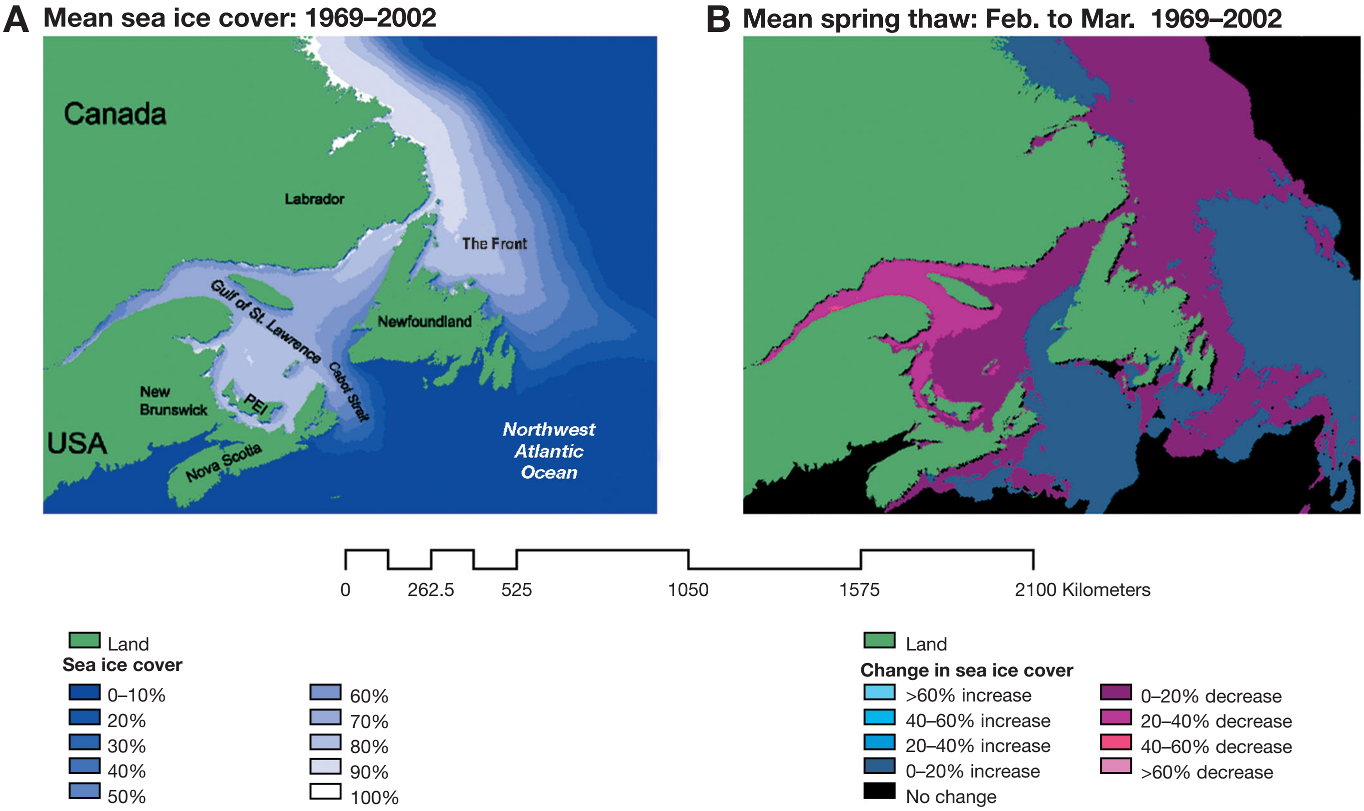

Fig. 5. (A) Spatial mean sea ice cover and (B) mean spatial changes in sea ice cover during the spring thaw, for 1969 through 2002. (A) White represents 100% sea ice cover and dark blue represents 0% sea ice cover. (B) Pink represents reductions in sea ice cover, while blue represents increases in ice cover

Table 1. General spatial patterns in yearly sea ice cover anomalies and reductions in sea ice cover during the spring thaw for eastern Canada during 1970, 1972, 1981, 1985, 1993 and 2001

Year	Fig.	Overall ice cover	Negative anomalies	Positive anomalies	Spring thaw (Feb to Mar)	FM NAO Index
1970	6A	Light	*Substantial:* western and north Gulf; east Newfoundland/ Labrador	*Minimal:* southern Gulf; offshore Labrador	West and central Gulf	Negative
1972	6B	Heavy	*Minimal:* offshore regions from Nova Scotia to Labrador	*Substantial:* entire Gulf; northern Newfoundland	Southern Gulf; offshore Labrador	Positive
1981[a]	6C	Light	*Substantial:* entire NE coast of Canada	*Minimal:* small area offshore Labrador	Entire Gulf and eastern Newfoundland	Negative
1985[b]	6D	Heavy	*Minimal:* western Gulf; south-central Newfoundland; offshore regions	*Substantial:* Cabot Strait, west and eastern Newfoundland/Labrador	West and central Gulf and eastern Newfoundland	Positive
1993	6E	Heavy	*Minimal:* offshore regions from Nova Scotia to Labrador	*Substantial:* entire Gulf; coastal Newfoundland/ Labrador	Western Gulf; eastern Newfoundland/ Labrador	Positive
2001	6F	Light	*Substantial:* west and north Gulf; eastern Newfoundland/ Labrador	*Minimal:* coastal Prince Edward Island, Newfoundland/Labrador	Western Gulf, northern Newfoundland/ Labrador	Negative

[a]Identified by Sergeant (1991) as a light ice year and small size-class of harp seals
[b]Identified by Sergeant (1991) as a heavy ice year

diminishing seaward (30 to 60%), and south off NE Newfoundland. The Gulf of St. Lawrence was almost completely covered in moderate concentrations of sea ice (>50%) with the area north of Prince Edward Island highly covered in ice (80 to 90%). As the spring thaw occurred, there were both reductions and increases in sea ice concentrations (Fig. 5B). Mean sea ice cover decreased in most of the Gulf of St. Lawrence, and off NE Newfoundland. Increases in sea ice cover during the spring thaw occurred in Cabot Strait, off the SE tip of Newfoundland, and in the open waters of the North Atlantic directly NE of Newfoundland.

The spatial analysis of anomalous light ice years revealed that yearly negative sea ice anomalies occurred in the Gulf region and off NE Newfoundland (Fig. 6A,C,F), the general patterns of which are presented in Table 1. During the spring thaw in light ice years, reductions in sea ice cover occurred in the Gulf and off Newfoundland and Labrador. In years with anomalously high ice cover, the pattern was relatively consistent (Fig. 6B,D,E). Generally, nearly all of the Gulf of St. Lawrence and coastal areas east of Newfoundland and Labrador exhibited positive anomalies in yearly sea ice cover. In spring thaw during heavy ice years, sea ice reductions were seen primarily in the western and southern Gulf of St. Lawrence, and to a lesser extent off eastern Newfoundland and Labrador.

4. DISCUSSION

The results of our analyses indicate that spring sea ice cover in the breeding regions of harp and hooded seals in eastern Canada has varied widely during the period 1969 to 2002. Our analyses detected the presence of extremely light ice years, in particular 1969 and 1981, both of which have been identified in earlier studies as light ice years (Sergeant 1991). It also revealed a recent string of light ice years, from 1996 to 2002. Our analysis also detected several years which exhibited heavy ice cover, in particular 1972, 1985, 1993 and 1994. Sergeant (1991) also previously identified 1985 as a heavy ice year in this region.

Sea ice, as a whelping substrate, is not simply a substitute for land (Fay 1974). It confers particular advantages to pagophilic seals, including protection from predators, greater haul-out space, variety in substrate, food supply, sanitation (in terms of disease and parasite transmission) and shelter (Fay 1974). Several of these functions can be affected by changes in sea ice cover and its duration. Those relevant to harp and hooded seals in eastern Canada are discussed below.

4.1. Yearly variation

The numerical analysis indicates that sea ice cover has varied widely over the past 33 yr, with few years close to the mean for the overall period (Fig. 1). Sea ice cover in our study area appears to vary periodically, with positive and negative extremes approximately 6 yr apart (Fig. 2B). The most recent negative period (1996 to 2002) is similar to negative periods that occurred in the early 1980s. The spatial analysis of extreme anomalies (Figs. 5 & 6) reveals that changes occur primarily in the Gulf of St. Lawrence but have also occurred off the east coast of Newfoundland, suggesting that both areas react similarly to seasonal shifts and climatic variation.

As described above, our study area sits between 2 geographical regions at opposite ends of a North–South dipole in NAO-induced climate effects. Our results suggest that the breakpoint for this dipole is south of our study area, as mean sea ice dynamics in eastern Canada appear to conform more closely to patterns associated with colder winters induced by positive phase winter NAO conditions.

Much of the period covered by our analyses coincides with an extended positive phase of the FM NAO, where only 9 of 33 yr exhibited a negative NAO index value. The lowest FM NAO index occurred in 1969, which also exhibited extremely low ice cover. The FM NAO grew steadily with coincident increases in sea ice cover until 1974, when it began to oscillate between higher and lower positive indices for much of the next 3 decades. As well, between 1984 and 1994 (the longest string of positive sea ice anomalies) only 2 years (1985 and 1987) had negative FM NAO index values. Most recently (1996 to 2002), a string of light ice years coincided with several large reductions in the FM NAO index, yet there were also strong positive values for the FM NAO during this period.

While the correlation between sea ice cover and FM NAO was not particularly strong, our results suggest that some of the variability in sea ice concentration may stem from changes in the winter NAO over the same period. These results are consistent with other relationships between sea ice cover and winter NAO phase in the western North Atlantic. For example, Deser et al. (2000) found positive correlations between sea ice concentration and winter NAO phase in the Labrador Sea, and Visbeck et al. (2003) showed that increased sea ice cover off eastern Newfoundland was also correlated to positive winter NAO phases.

Yearly variation in sea ice cover may have significant effects on harp and hooded seals. For example, in light ice years the quantity of ice that is appropriate for whelping can be greatly reduced, and female seals may crowd into whelping areas and produce pups in

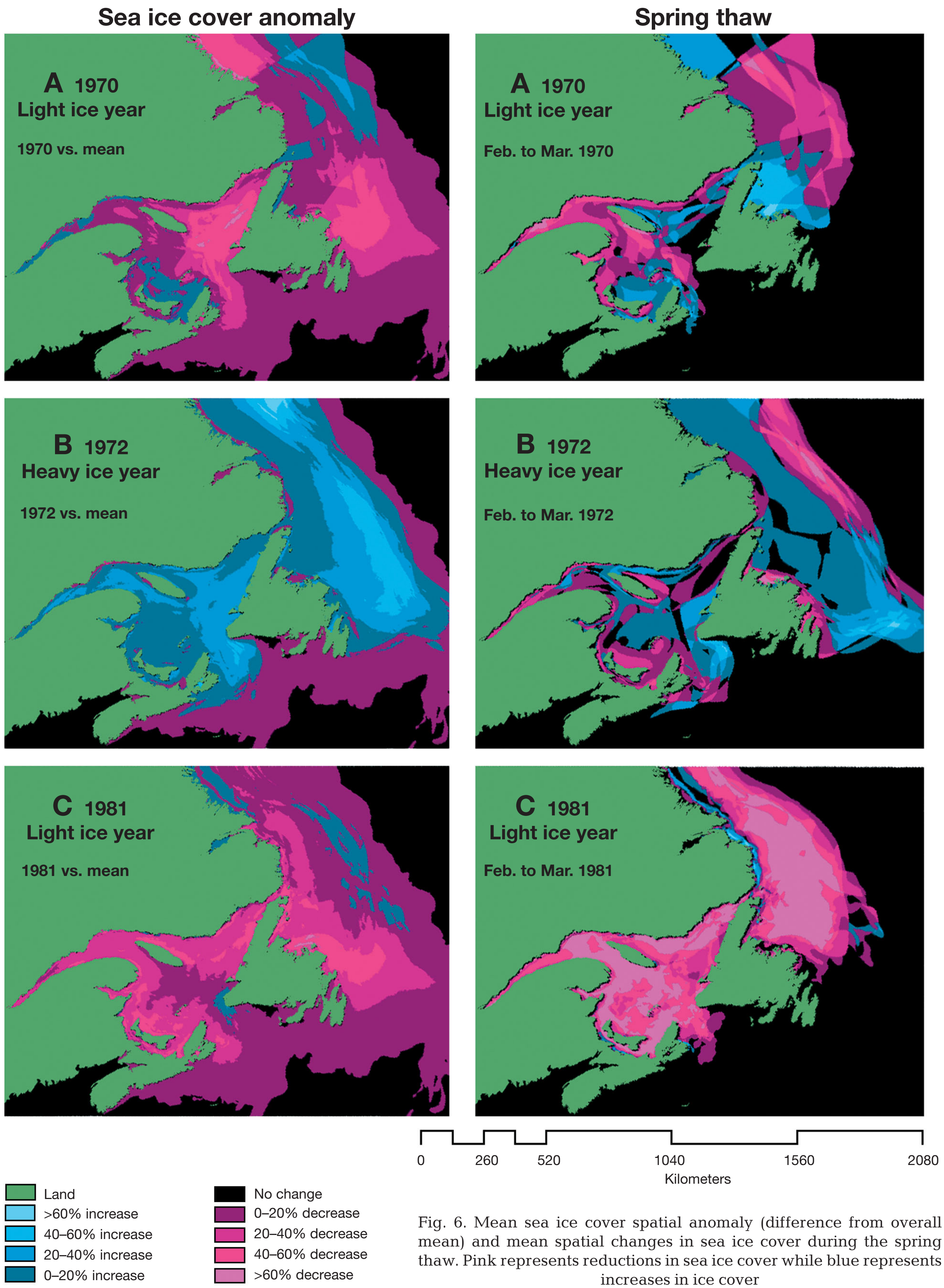

Fig. 6. Mean sea ice cover spatial anomaly (difference from overall mean) and mean spatial changes in sea ice cover during the spring thaw. Pink represents reductions in sea ice cover while blue represents increases in ice cover

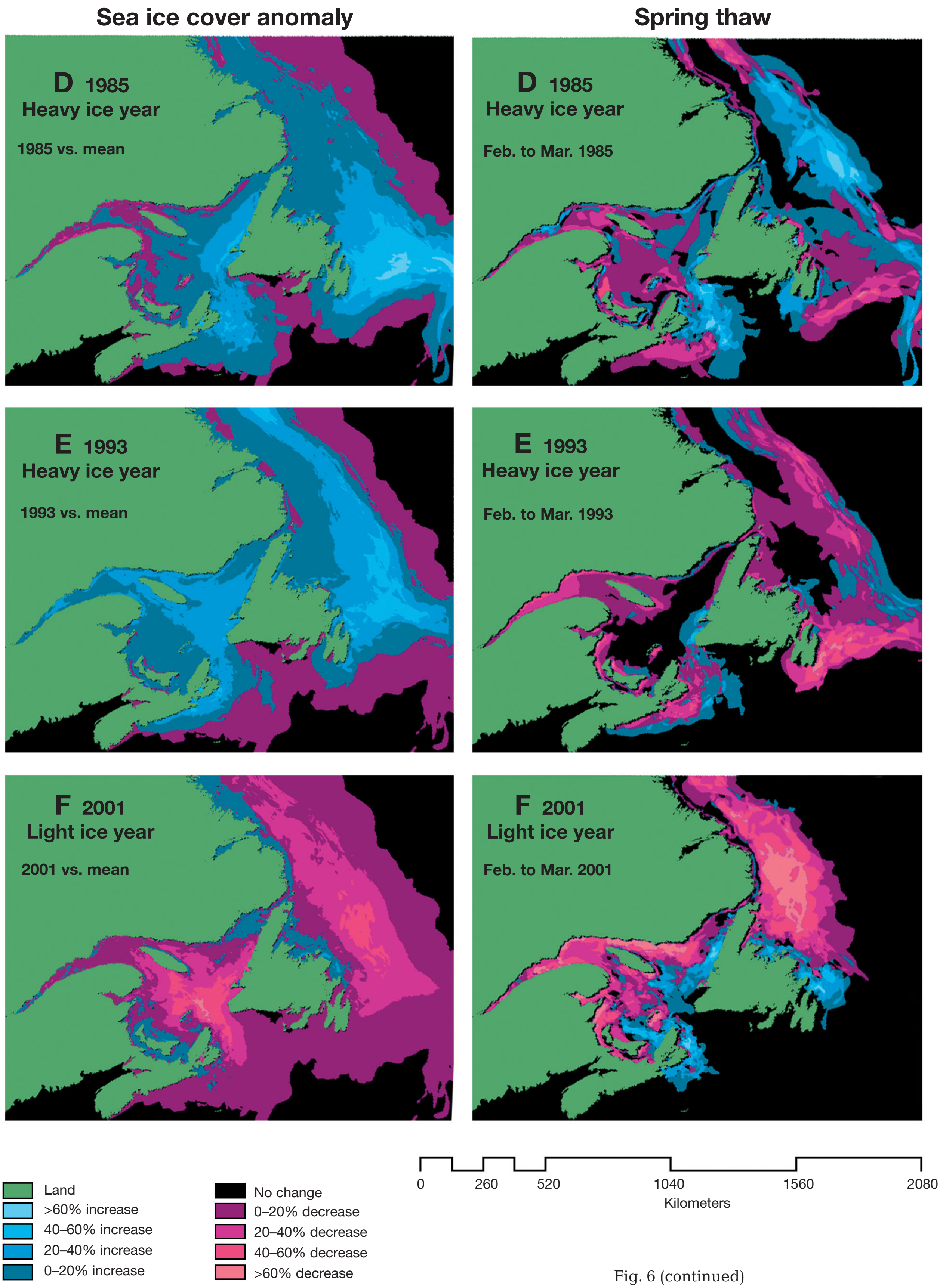

Fig. 6 (continued)

high densities. If such crowding occurred, it would increase the chances of disease transmission and subsequently the risk of epizootics (Fay 1974)—like morbillivirus outbreaks seen in other species of seals and small cetaceans (Lavigne & Schmitz 1990, Kennedy 1998, 1999). There is already evidence that pagophilic seals in the NW Atlantic are at risk to morbillivirus infections. For example, a large proportion of harp and hooded seals sampled from the western North Atlantic between 1989 and 1993 carried phocine distemper virus antibodies (Duignan et al. 1997), and phocine distemper has been recorded in a stranded juvenile harp seal in the Gulf of St. Lawrence (Daoust et al. 1993).

Although the effects of crowding by reproductive harp and hooded seals at whelping patches in eastern Canada is largely unknown, crowding on sea ice is known to have negative effects on other pagophilic seal populations. For example, increased predation by Pacific walruses *Odobenus rosmarus divergens* on ringed seal *Pusa hispida* pups in the Bering Sea during 1979—a very light ice year—was likely due to crowding of both species on available ice (Lowry & Fay 1984).

4.2. Variation in spring thaw

Both the numerical and spatial analyses clearly illustrate the effects of the spring thaw on sea ice coverage in the Gulf of St. Lawrence and on the Front over the duration of the study. The spatial analysis of mean spring thaw illustrates the locations contributing to the significant decrease in mean sea ice cover between February and March (Fig. 5B). Interestingly, it appears that during the spring thaw sea ice cover tends to increase in 2 areas. These appear to be areas that sea ice is transported to and where it accumulates during the spring thaw in shelf-break and geostrophic fronts or restriction points in residual current patterns.

The numerical analyses indicate that in light sea ice years (e.g. 1970, 1981, 1999, 2001) there was a rapid reduction in ice cover in the study area in the first or second week of March, a phenomenon that was not observed in heavy ice years (Fig. 4). The spatial analysis for these years reveals that the changes occurred primarily in the Gulf, but also on the Front (especially in 1981; see Fig. 6C, spring thaw). The timing of the spring thaw is important for harp and hooded seals as variability in where and when sea ice degrades at whelping patches can have consequences for nursing or recently weaned pups. Young harp seal pups are generally poor swimmers and have limited blubber stores for insulation (Lavigne & Kovacs 1988). Animals that are nursed on rapidly degrading sea ice may suffer from cold stress or starvation if they must enter the water prematurely, greatly reducing their chance of survival. Moreover, juvenile and adult animals are sometimes crushed by shifting ice (Lavigne & Kovacs 1988). The mean birthing date for harp seals in the Gulf of St. Lawrence occurs around March 1 to 5 (Stewart 1987), and birthing is delayed in the Front region by about 5 d (Sergeant 1991). Harp seals lactate for approximately 12 d (Kovacs et al. 1991), after which the pups are weaned and abandoned. Hooded seals usually whelp in the second half of March, with a lactation period of only 4 d (Bowen et al. 1985). The timing of these events is coincident with the rapid reductions in sea ice cover seen in both the Gulf and Front regions during light ice years. Therefore, limited ice availability in these years may have significantly increased neonatal mortality in harp and hooded seals in eastern Canada. The occurrence of interrupted nursing periods resulting from reduced sea ice cover has been previously recorded for ringed seals in western Prince Albert Sound, NT, Canada (Harwood et al. 2000).

The effect of light sea ice conditions on neonatal and juvenile mortality has not been studied specifically for harp and hooded seals in eastern Canada. However, Sergeant (1991) reported an extremely small sized 1981 year-class of harp seals (revealed in subsequent age-class samples collected from a seal hunt in the Gulf of St, Lawrence during 1984–1985), which was likely due to light ice conditions and extremely high juvenile mortality. Our analysis confirms that 1981 was a light ice year (Figs. 1 & 6C, sea ice cover anomaly), with a rapid reduction in sea ice cover in the Gulf starting in the first week of March (Fig. 4C) that left large numbers of pups dead from starvation or cold stress on the shores of Prince Edward Island (Sergeant 1991). The ice dynamics for 1981 were similar to those recently ooccuring (1998 to 2002) in the Gulf of St. Lawrence (Figs. 1, 4F & 6F), although the reduction in sea ice cover was more extreme in 1981. This supports the hypothesis that juvenile mortality in some recent years (e.g. 2002) has also been up to 5 times higher (Anonymous 2003). Also consistent with this hypothesis are the reports of dead pups washed up on the shores of Prince Edward Island and Cape Breton in 1998 and 1999 (Toughill 1998, Anonymous 1999), both light ice years.

Changes in ice coverage may have indirect affects on seals as well. A large and significant amount of primary productivity in ice-covered oceans takes place under sea ice or in blooms associated with sea ice margins (Garrison et al. 1987). In some areas in the North Atlantic and North Pacific, primary productivity associated with sea ice and sea ice margins can be high and contributes significantly to overall production (McRoy & Goering 1974, Horner & Schrader

1982, Slagstad 1984). Ice cover may be important in areas where it increases stratification by reducing wind-driven mixing in the upper portion of the water column or where stratification occurs because of fresh water release as ice melts (Slagstad 1984). As light levels increase in spring, phytoplankton communities associated with sea ice and the sea ice margin bloom greatly increase local productivity. Recently weaned harp seals are poor swimmers and depend primarily on invertebrate prey (Stewart & Lavigne 1980, Martensson et al. 1994) as they learn to forage, the availability of which is dependent on local primary production. Rapid changes or extremes (both high and low) in sea ice cover in the Gulf of St. Lawrence or on the Front may affect the timing and magnitude of early spring plankton blooms and, subsequently, secondary production in the region. This in turn may alter the availability of prey for recently weaned seal pups. Ringed seals in the Arctic depend heavily on sea ice productivity for survival (Bradstreet & Cross 1982) and Lowry (2000) suggested that decreases in ice cover or duration could reduce availability of their prey. Conversely, Harwood & Stirling (1992) suggest that the reduced productivity of ringed seals in the eastern Beaufort Sea during the 1970s and 1980s may have stemmed from reduced primary productivity due to heavier than normal ice cover. Clearly, more research into changes in sea ice and sea ice margin productivity in eastern Canada is required to better understand how they may affect prey availability for harp and hooded seals, especially young-of-the-year individuals.

4.3. Climate change and variability, and pagophilic seals

There is growing interest in incorporating the effects of climate variability into ecological research (Stenseth et al. 2003).There are several studies correlating NAO variability in North America with the abundance, behaviour and population synchrony in ungulates (Post & Stenseth 1999), mustelids (Haydon et al. 2001), wolves (Post et al. 1999) and large cats (Stenseth et al. 1999). Significant changes in cohort demographics related to NAO variability have also been found in terrestrial mammals in Europe, the most intensively studied examples being red deer *Cervus elaphus* in Norway (e.g. Forchhammer et al. 1998) and Soay sheep *Ovis aries* in the St. Kilda Archipelago, Scotland (Forchhammer et al. 2001). There are few studies relating NAO variability to marine mammal biology or ecology, a notable exception being a link between right whale *Eubalaena glacialis* prey and NAO effects on slope water in the Gulf of Maine (Drinkwater et al. 2003, Greene et al. 2003).

Our analyses suggest that the dominance of positive winter NAO phases between 1982 and 1995 might have been beneficial for reproductive harp and hooded seals, as positive sea ice cover anomalies in eastern Canada (and subsequently sea ice persistence through the spring thaw) are correlated with the positive FM NAO index. While this may be true for 1982 through 1995, we recommend caution in extending this interpretation to more recent and future seasons, or to other populations of pagophilic seals. In our case, the effects of global climate change on sea ice in eastern Canadian waters may actually be buffered by the recent dominance of positive winter NAO conditions. While both the extent and thickness of sea ice cover appear to have decreased significantly throughout the Arctic (Johannessen et al. 1999), there is evidence of slight increases in sea ice cover in the Davis Strait/Labrador Sea region during 1950 to 1995, due to the recent dominance of positive NAO conditions (Chapman & Walsh 1993, Visbeck et al. 2003). If NAO conditions switch dramatically to an extended negative phase, we may see greater reductions in the availability of sea ice for pagophilic seals in eastern Canada. Several studies have noted latitudinal changes in climate in North America associated with global climate change, with a northward shift in warmer temperatures and associated changes in natural history and the distributions of some species of plants and animals (see Parmesan & Yohe 2003, Root et al. 2003). If a similar climate shift was to occur in our study area, or the North–South dipole in NAO effects were to shift northwards, eastern Canada would likely experience warmer, wetter winter conditions and subsequently reduced ice cover.

An analysis of recent trends (1981 to 2001) in seasonal mean surface temperatures in the Arctic obtained from thermal satellite sensors reveals that areas in the eastern Arctic south to Davis Strait and the Labrador Sea (portions of the summer habitat of harp seals; Lavigne & Kovacs 1988) have actually warmed recently (Comiso 2003). An examination of yearly mean surface temperature grids reveals that most of the warming appears to have occurred during 1995 to 2001 (Comiso 2003). This corresponds well with the most recent string of negative sea ice anomalies detected in our analyses (1996 to 2002). It also corresponds with the portion of our time series analysis that is least correlated with the FM NAO. Further research (and a longer times series) is required to determine whether this represents a northward dipole shift as described above, or a separation of the link between positive NAO phases and heavy ice years in eastern Canada. Regardless of the proximate mechanism responsible for recent warming in the Labrador Sea/ Davis Strait region, it is becoming clear that changes in climate may also pose risks for non-reproductive harp seals, which associate with sea ice throughout the summer in northern Canadian waters (Lavigne & Kovacs 1988), and for hooded seals using a winter breeding site in Davis Strait (Lavigne & Kovacs 1988).

Three populations of harp seals are recognized (Lavigne 2002), one population whelps on ice in eastern Canada, the second whelps on sea ice off east Greenland (West Ice) and the third on sea ice in the White Sea (Lavigne & Kovacs 1988). Changes in winter NAO conditions, and subsequently sea ice cover, may have significant effects on the latter populations as well. For example, Chapman & Walsh (1993) and Visbeck et al. (2003) indicate that sea ice cover in the Greenland Sea — and to a lesser extent in portions of the White Sea — was negatively correlated with positive winter NAO conditions and has seen a decline of 3 to 6% between 1950 and 1995. Research into these reductions (and potential sea ice anomalies like those we report here) and their effects on West Ice and White Sea harp seals is required to understand how climate variability and climate change may affect pagophilic seals in locations beyond eastern Canada.

Harp and hooded seals are not the only species of seal known to use ice as a breeding platform in eastern Canadian waters. Grey seals *Halichoerus grypus* also whelp on ice in the Gulf of St Lawrence and the St. Lawrence River Estuary (Mansfield & Beck 1977), and grey seal pups would likely share some of the same risks posed by variation in ice cover in their breeding areas.

4.4. Implications for management

Sea ice cover has varied widely in the NW Atlantic over the past 33 yr, with coincident changes in breeding habitat for harp and hooded seals. While the extent to which these changes affect seal populations remains largely unstudied, the available data suggest that light ice years, partially induced by lower winter NAO index values, are likely to result in increased mortality, particularly among young-of-the-year seals. As well, reductions in available whelping habitat may increase the risk of disease transmission among adult and juvenile seals. Increased pup mortality may have been especially important between 1996 and 2002, when sea ice cover was light, catch limits for harp seals were increased, and unsustainable removals from the population occurred (Lavigne 1999, Johnston et al. 2000).

Our results have implications for management in at least 3 ways. (1) The significant link between sea ice cover and the FM NAO index can be exploited to alter management decisions rapidly, before quotas are set. In situations where the winter NAO index is low, managers could elect to reduce impending quotas for younger seals (now set 3 yr in advance; see Anonymous 2003) to help mitigate the effects of poor ice years. (2) Data on light ice years and NAO anomalies may be useful in forecasting when to alter seal hunt quotas to account for poor year-classes returning to the ice to whelp. Harp seals begin to reach sexual maturity at about 4 yr, hooded seals at 3 yr, after which they return to whelping patches yearly to pup (Lavigne & Kovacs 1988). In situations where several poor year-classes are expected at whelping patches (due to repeated light ice years and increased pup mortality), maintaining reduced hunting pressure on adult seals could help to ensure that weak year-classes do not become overexploited. (3) Data on the frequency and effects of sea ice variation on seal populations could be factored into models designed to estimate ecologically sustainable removal levels. For example, incorporating changes in pup mortality from sea ice variation into simulations of population dynamics over time, under various exploitation scenarios (e.g. Wade 1998), can allow scientists to fine-tune models and managers to optimize conservation goals and exploitation levels.

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